Citation:

Talbot, J., et al. (2014), Methods to estimate aboveground wood productivity from long-term forest inventory plots, For. Ecol. Manage., 320, 30-38, doi:10.1016/j.foreco.2014.02.021.

Methods to estimate aboveground wood productivity from long-term forest inventory plots

Joey Talbot[a*], Simon L. Lewis[a,b], Gabriela Lopez-Gonzalez[a], Roel J.W. Brienen[a], Abel Monteagudo[c], Timothy R. Baker[a], Ted R. Feldpausch[1], Yadvinder Malhi[d], Mark Vanderwel[e,f], Alejandro Araujo Murakami[g], Luzmila P. Arroyo[g], Kuo-Jung Chao[a,h], Terry Erwin[i], Geertje van der Heijden[j,k], Helen Keeling[a], Tim Killeen[g], David Neill[l], Percy Nunez Vargas[m], Germaine Alexander Parada Gutierrez[g], Nigel Pitman[n], Carlos Alberto Quesada[o], Marcos Silveira[p], Juliana Stropp[q] and Oliver L. Phillips[a]

[a]*School of Geography, University of Leeds, Leeds, LS2 9JT, UK*

[1]*Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK*

[b]*Department of Geography, University College London, Pearson Building, Gower Street, London, WC1E 6BT, UK*

[c]*Jardín Botánico de Missouri, Oxapampa, Pasco, Peru*

[d]*Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK*

[e]*Computational Ecology and Environmental Science Group, Microsoft Research, 21 Station Road, Cambridge, CB1 2FB, UK*

[f]*Department of Biology, University of Florida, Gainesville, FL, USA*

[g]*Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia*

[h]*National Chung Hsing University, Taiwan*

---

* Correspondence author. Email: gyjt@leeds.ac.uk.

Tel: +44 113 343 9448

[i]*Department of Entomology, National Museum of Natural History, Smithsonian Institution, MRC 187, P.O. Box 37012, Washington, DC 20013, USA*

[j]*University of Wisconsin-Milwaukee, P.O Box 413, Milwaukee WI 53201, USA*

[k]*Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panama*

[l]*Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador*

[m]*Universidad Nacional San Antonio Abad del Cusco, Av. de la Cultura 733, Cusco, Apartado Postal No 921, Peru*

[n]*Center for Tropical Conservation, Nicholas School of the Environment, Duke University, Box 90381, Durham, NC 27708-0381 USA*

[o]*Instituto Nacional de Pesquisas na Amazônia, Av. Andre Araujo, 1753 CP 478, 69060-011 Manaus AM, Brazil*

[p]*Universidade Federal do Acre, Depto de Ciencias da Natureza, Rio Branco AC 69910-900, Brazil*

[q]*Joint Research Centre of the European Commission, Institute for Environment and Sustainability, via Enrico Fermi 2749, I-21027, Ispra, Italy.*

Abstract

Forest inventory plots are widely used to estimate biomass carbon storage and its change over time. While there has been much debate and exploration of the analytical methods for calculating biomass, the methods used to determine rates of wood production have not been evaluated to the same degree. This affects assessment of ecosystem fluxes and may have wider implications if inventory data are used to parameterise biospheric models, or scaled to large areas in assessments of carbon sequestration. Here we use a dataset of 35 long-term Amazonian forest inventory plots to test different methods of calculating wood production rates. These address potential biases associated with three issues that routinely impact the interpretation of tree measurement data: (1) changes in the point of measurement (POM) of stem diameter as trees grow over time; (2) unequal length of time between censuses; and (3) the treatment of trees that pass the minimum diameter threshold (“recruits”). We derive corrections that control for changing POM height, that account for the unobserved growth of trees that die within census intervals, and that explore different assumptions regarding the growth of recruits during the previous census interval. For our dataset we find that annual aboveground coarse wood production (AGWP; in Mg dry mass ha^{-1} year^{-1}) is underestimated on average by 9.2% if corrections are not made to control for changes in POM height. Failure to control for the length of sampling intervals results in a mean underestimation of 2.7% in annual AGWP in our plots for a mean interval length of 3.6 years. Different methods for treating recruits result in mean differences of up to 8.1% in AGWP. In general, the greater the length of time a plot is sampled for and the greater the time elapsed between censuses, the greater the tendency to underestimate wood production. We recommend that POM changes, census interval length, and the contribution of recruits should all be accounted for when estimating productivity rates, and suggest methods for doing this.

Key words: aboveground coarse wood production, biomass, carbon, census interval, diameter, tropical forest

1 Introduction

The role of forests in carbon cycling has gained increasing attention in recent years. Globally, forests represent a carbon stock of 861 ± 66 Pg C, with 42% of this in live biomass (Pan et al., 2011). The greatest carbon stocks and fluxes are found in the tropics, with major impacts associated with both natural processes and anthropogenic land-use change activities. Tropical forests contain an estimated 55% of global forest carbon (Pan et al., 2011) and account for 34% of terrestrial gross primary production (Beer et al., 2010). Between 1990 and 2007, tropical intact forests were estimated to represent a carbon sink of 1.2 ± 0.4 Pg C year^{-1}, of similar magnitude to the net anthropogenic carbon loss in tropical forests due to deforestation and secondary regrowth (Pan et al., 2011).

Methods for estimating aboveground live carbon stocks from discrete permanent sample plots are relatively well-established in tropical forests, with different plot networks having largely converged on common field methods (e.g., Condit, 1998; TEAM Network, 2010; Phillips et al., 2009a) and similar analytical techniques (e.g., Chave et al., 2008; Lewis et al., 2013; Phillips et al., 2009b). However the estimation of aboveground wood production from the same type of long-term plots has not been given the same degree of attention. For all ecologists interested in understanding and comparing key aspects of forest ecosystem functioning, as well as for forest management, the quantification of atmosphere-biosphere carbon fluxes and the effects of climate variability on forest productivity (Tian et al., 1998), having access to reliable and comparable estimates of wood production is critical. For example, wood production must be accurately estimated in order to assess the role that tropical forests appear to play in buffering the increase in atmospheric CO_2 concentration caused by human activity. In future the carbon uptake of tropical forests could be reduced or even reversed (Huntingford et al., 2013), and if this were to occur by warming or drying it could lead to positive feedback further enhancing climate change (Friedlingstein et al., 2006).

Our interest lies in coarse wood production, as the major long-lived component of net primary production (NPP). As the portion of gross primary production (GPP) that is not lost in respiration, NPP is determined by both GPP and carbon use efficiency. Components of NPP include aboveground and belowground wood production; leaf, flower, and fruit production; fine root production; and the production of volatile organic carbon compounds and root exudates (Malhi et al., 2011). Coarse wood production represents tissues that contribute to the long-term storage and sequestration of biomass carbon, and is also the component with the greatest relevance to forestry studies (Blanc et al., 2009). For these and practical reasons most inventory plot studies measure the aboveground fraction of coarse wood production (AGWP).

The estimation of AGWP normally involves the repeated measurement of stem diameter (D) for all stems within a defined area (an inventory plot), across a number of census intervals. Aboveground biomass (AGB) estimates for each census are obtained using allometric equations. However there remains no single agreed method for the derivation of AGWP from these repeated measures. Although here we consider solely methodological effects on productivity estimation, equivalent methods can also, if required, be used for the calculation of losses of live coarse wood from the system through mortality. This will avoid any apparent imbalances in net fluxes being driven by methodological artefacts.

To obtain the most accurate estimates of AGWP it is preferable to use a long sampling period. This reduces the signal-to-noise ratio, minimising the impact of hydrostatic flex that may affect the measurement of some trees (Sheil, 1995), and minimising small measurement errors, which can have disproportionate influence across short census intervals. It also ensures that AGWP estimates represent an average of different years with different conditions, reducing uncertainties relating to the impacts of short-lived disturbances and stochastic mortality events, as well as potentially larger-scale events such as droughts or insect outbreaks. Long sampling periods therefore enable more accurate comparisons between plots. However, long sampling periods and long intervals between individual censuses also increase the chance of encountering problems associated with three factors that affect AGWP estimation, as explained below.

Firstly, individual trees naturally tend to increase in height, stem and crown diameter over time. As a tree grows, the need for stabilisation is satisfied in many tropical species by progressive development of root buttresses. Other species may have adventitious or prop roots that move upwards through time. The point of measurement (POM) for stem diameter is normally set at 1.3m or a fixed height above buttresses, but as deformities creep up the trunk, POM changes are often necessary (Sheil, 1995). These will affect an increasing number of trees with increasing time elapsed since the first measurement. The new POM will typically be at a higher point, where the stem has lower *D* due to stem taper (Fang and Bailey, 1999). The existence of stem taper, which can vary greatly between species (Poorter and Werger, 1999), means that *D* measurements taken at different POMs are not directly comparable, and treating them as such would bias growth estimates (King, 1981; Niklas, 1995). Procedures are therefore required to correct for this impact.

Secondly, the unobserved growth of trees that subsequently die within an interval represents a source of bias closely related to interval length (Sheil and May, 1996). The longer the interval, the more unobserved growth there will be, both from previously measured stems and from unmeasured stems that pass the minimum diameter threshold and subsequently die within the same interval unrecorded (Lewis et al., 2004; Malhi et al., 2004; Sheil and May, 1996). Clearly the relative importance of this effect increases with increasing census interval length.

A third origin of uncertainty in AGWP measurements is the approach used to deal with recruits, i.e. those trees that have reached the minimum measured *D* threshold by the end of a given census interval. Since these trees were not measured at the start of the interval, their growth within the interval is unknown. Two common approaches have been used: assuming growth over the interval is only that greater than the diameter measurement threshold in the study (typically 10 cm; i.e. a new recruit of 11 cm is assumed to have grown 1 cm); or recruits were 0 cm in the previous census interval (Clark et al., 2001; Malhi et al., 2004). The fraction of AGWP associated with recruits, and the concomitant degree of uncertainty, will increase with mean census interval length.

Other factors could influence productivity estimates, for example the choice of procedures used to deal with missing or extreme values, the choice of allometric equation, the carbon fraction (Martin and Thomas, 2011), the belowground: aboveground biomass ratio assumed (Deans et al., 1996) and estimation of wood density (Flores and Coomes, 2011). These are important concerns but beyond the scope of this paper's focus on methodological considerations related to processing accurately collected data.

We present procedures developed to minimise the biases associated with POM changes and census interval length, and make explicit how the treatment of recruits can alter results, using a large number of forest plots to assess impacts on AGWP rates. We review a set of methods for AGWP estimation, evaluate the biases, and provide recommendations for the estimation of AGWP from permanent sample plots in tropical forest.

2 Materials and Methods

Thirty five long-term forest inventory plots from Western Amazonia were selected from a single database (www.forestplots.net, Lopez-Gonzalez et al., 2011), all part of the RAINFOR network. To ensure that plots were appropriate for the investigation of how methodologies for POM changes, census interval length and recruitment affect productivity, we used only plots with at least three censuses over a period of at least 10 years, using only censuses where the POMs had been recorded in the database by the authors. To ensure accurate wood density values could be used, we selected plots that had been visited by a botanist, with >80% of stems identified to genus level (mean 97%). All plots were in mature old-growth forests. Plot size ranges from 0.88 ha to 1 ha, with mean number of census intervals of 4.9 and mean interval length of 3.6 years. The sites span lowland Western Amazonia, from seasonal forests near the savanna margins in the south to the wet upper Amazon. The selected plots are listed in Table S1.

We estimated the aboveground biomass (AGB) of each stem ≥10 cm *D* at each census, including monocotyledons which we treated in the same way as dicotyledons. We estimated AGB using the Chave et al., (2005) moist forest equation, $AGB = exp\ (-2.977 + ln\ (\rho D^2H))$, where *D* is stem diameter (in cm) at reference height, *H* is the height of the stem (in m) and ρ is stem wood density (in g cm^{-3}) (Figure 1). Height was inferred from diameter using the regional height-diameter Weibull equation of Feldpausch et al., (2012). We estimated the wood density of individual stems using a pan-tropical database (Chave et al., 2009; Zanne et al., 2009). The most resolved taxonomic level available was used, following the method of Lewis et al., (2009), using continent-specific wood density taxon reference values.

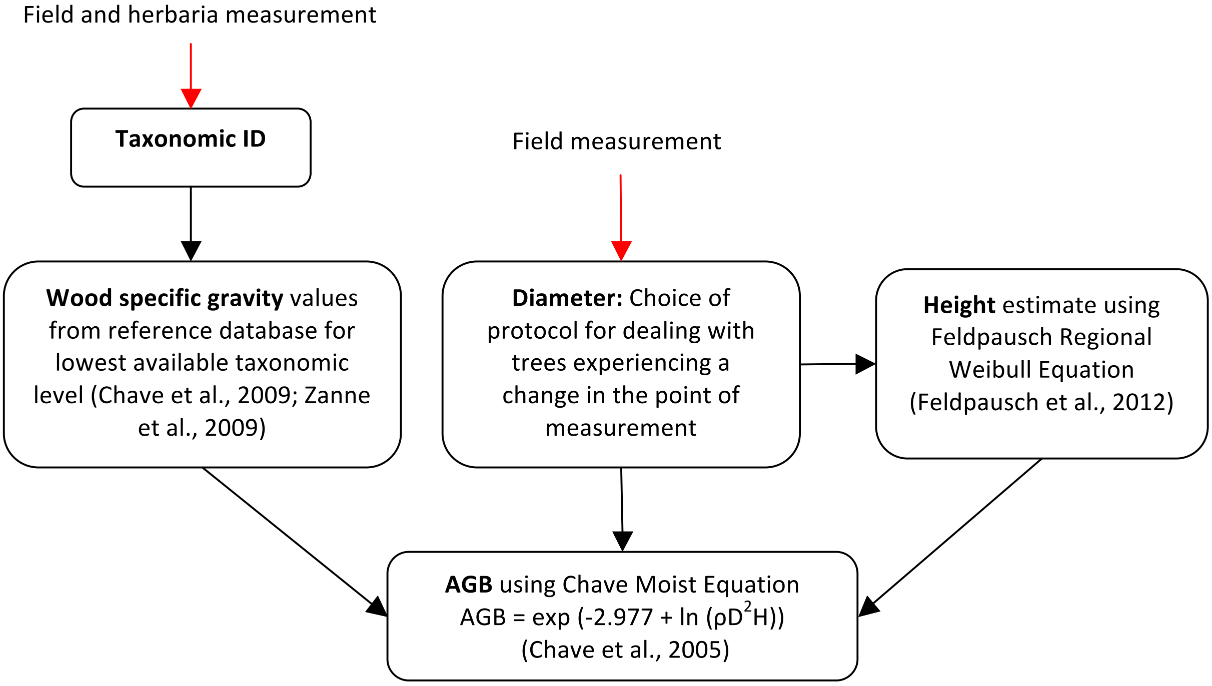

Figure 1: Procedure for estimating the AGB of a single stem.

Diameter was measured for all stems with *D* ≥10 cm, using diameter tape at a height of 1.3 m, or above buttresses or other stem deformities. When such deformities threatened to encroach the current POM we changed to a new POM, recording the diameter at both the old and new POMs. Stem taper can be estimated by the ratio of *D* at old POM (D_{old}): *D* at new POM (D_{new}). We used this ratio to calculate standardised estimates of D_{old} for each census after a POM change and of D_{new} for each census prior to a POM change, with D_{mean} denoted as the mean of D_{old} and D_{new} (Figure 2).

We used a number of techniques to avoid or minimise potential errors arising from missing diameter values, typographical errors, or extreme *D* growth ≥4 cm year^{-1} or total *D* growth ≤-0.5 cm across a single census interval (i.e. losing 0.5 cm, as trees may shrink by a small amount due to hydrostatic effects in times of drought, and measurement errors can be both positive and negative). For stems belonging to species known to experience very high growth rates, or noted as having damaged stems, we accepted these values. We used interpolation, where possible, or extrapolation to correct errors. If neither of these procedures were possible we used the mean growth rate of all dicotyledonous stems in the same plot census, belonging to the same size class, with size classes defined as $10 \leq D < 20$ cm, $20 \leq D < 40$ cm, and $D \geq 40$ cm, to estimate the missing diameter value. Of all stem growth increments, 1.7% per census were assigned interpolated estimates of diameter, for 0.9% we used extrapolated estimates, and for 1.5% we used mean growth rates.

To estimate the AGWP of a given plot across a single census interval, we summed the change in AGB for each tree present at both the start and end of the interval, plus the AGB of new recruits present at the end of the interval, and divided the result by the interval length. Having calculated mean annual AGWP of each census interval, we then calculated mean annual AGWP across the entire period during which a given plot had been sampled, weighting the AGWP of each individual census interval by the length of the interval.

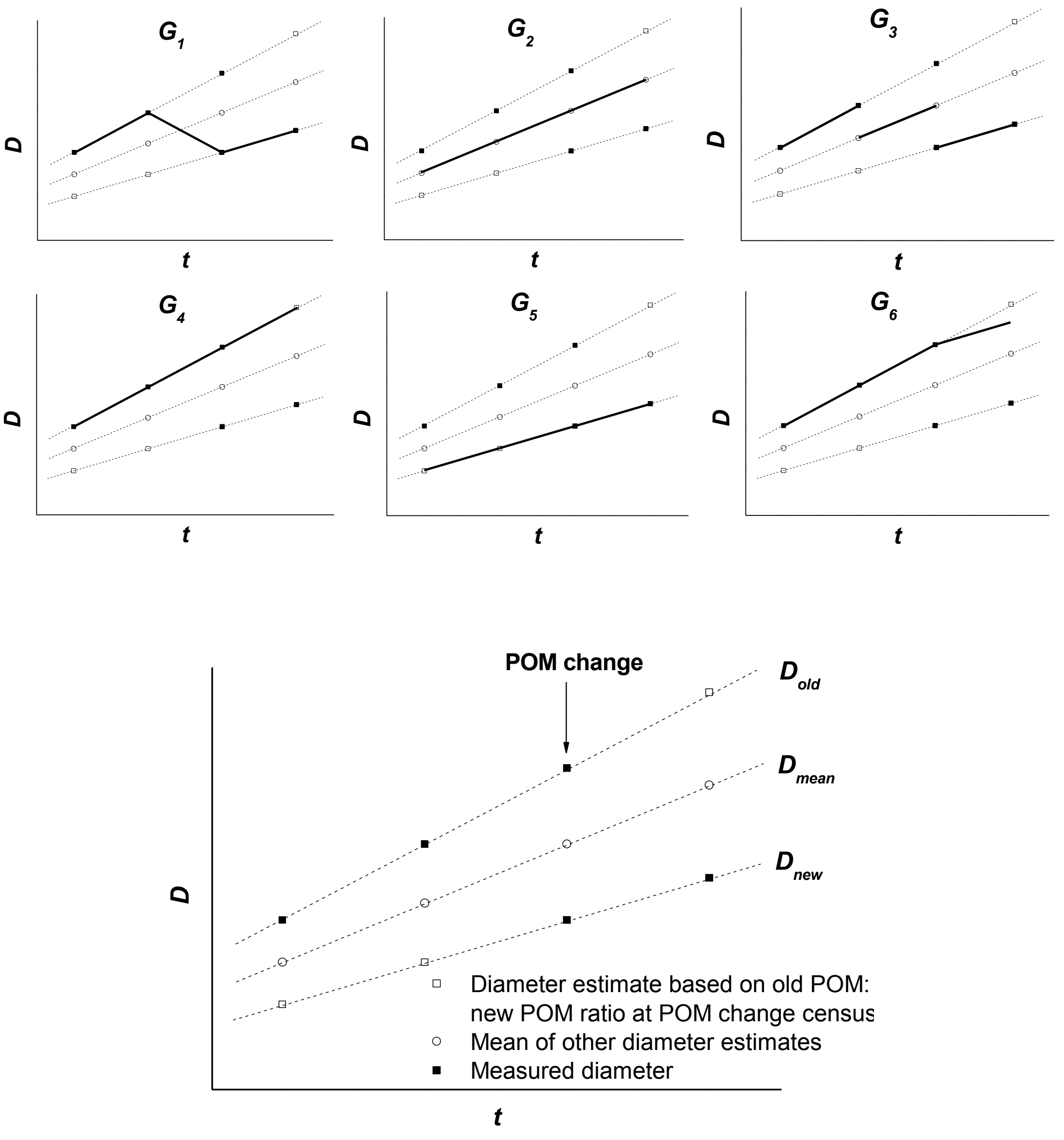

Figure 2: Diameter and growth measures for a hypothetical stem which has undergone a POM change. Growth measurement protocols are shown as the bold lines in the insets. G_1: *Uses measured diameter in all censuses, regardless of POM changes;* G_2: *Uses estimated diameter at a standardised POM height (*D_{mean}*) in all censuses, representing the mean of* D_{old} *and* D_{new}*;* G_3: *Uses a combination of estimated diameter at* D_{mean} *in censuses with POM changes and measured diameter in other censuses;* G_4: *Uses diameter at* D_{old} *in all censuses;* G_5: *Uses diameter at* D_{new} *in all censuses;* G_6: *After a POM change the increment at* D_{new} *is added to the original diameter at* D_{old}.

We used multiple methods to estimate wood production, in response to the three problems of POM changes, census interval length, and recruitment. These included a designated ‘suggested scenario’ involving corrections relating to POM changes and census interval length, and a ‘baseline scenario’ that lacked these corrections. We could thereby quantify how our AGWP estimates using other method combinations deviated from these two reference cases. Since our recommended treatment of recruits itself depends on the specific question being asked by a researcher, we used the same method of treatment of recruits in both the baseline and the suggested scenarios.

2.1 TREATMENT OF POM CHANGES

A number of approaches for treating POM change trees were tested to explore their impact on AGWP estimates (Figure 2). Our first method provides no correction for stems with POM changes (denoted ‘G_1’). This is used in our baseline scenario. At any given census, this is normally expected to provide the best measure of stem diameter at that particular census, and could therefore be appropriate for biomass estimation. However, when stems undergo POM changes, changing the height at which this diameter is taken, the existence of stem taper means that estimates of wood production will be biased downwards across these intervals.

To avoid the bias inherent in G_1 and to help quantify its impact, we explored five alternatives (Figure 2). In the second method, denoted ‘G_2’, we use the estimated diameter at a standardised POM height (D_{mean}) in all censuses, with D_{mean} representing the mean of D_{old} and D_{new}. The third method, ‘G_3’, uses a combination of techniques from G_1 and G_2. Thus, for all census intervals not involving a POM change, the directly measured diameters were used to calculate growth (as in G_1), but for census intervals involving a POM change, D_{mean} was used to calculate growth across that interval (as in G_2). G_3 is used in our suggested scenario. Our three final techniques are similar to G_2 in that they all maintain a constant POM height across all censuses for each tree. With G_4 this POM is at D_{old} in all intervals, with G_5 it is at D_{new} in all intervals, and with G_6, which follows the method of Clark et al., (2013), the measured diameter increment at D_{new} after a POM change is added to the original diameter at D_{old}.

2.2 TREATMENT OF DIFFERING CENSUS INTERVAL LENGTH

The longer a census interval, the greater the proportion of growth that will go unobserved within the interval. Census interval correction is required to account for two sources of error – unobserved growth from trees that were known to have died during the interval, and unobserved growth from trees that both recruited and died during the interval. We used two different methods to derive correction factors that accounted for the effects of census interval length on observed AGWP. In our results, the baseline scenario does not include any correction for census interval length, while our suggested scenario uses the second correction method.

First, we used a parametric technique based on the methods of Malhi et al., (2004), denoted 'CIC_1', but with the corrections applied to AGWP rather than basal area growth rates (as in Phillips et al., 2009b). For this, we calculated AGWP across all of the one-, two- and three-census periods within each plot, grouping consecutive censuses to create the two- and three-census periods. We included every possible combination of consecutive censuses within a given plot, except for those of greatly different lengths (ratios of 1: 3 or greater), which we excluded to minimise variation in the length of these intervals. Any censuses that we excluded in this way were excluded from the estimates of AGWP across all single censuses as well as the estimates of AGWP across the two- and three-census periods. We derived growth using G_2 to avoid problems associated with POM changes in the two- and three-census periods.

We then calculated the mean length and mean annual AGWP of all of the single censuses in a plot, all of the two-census periods, and - for plots with at least four censuses – all of the three-census periods. We regressed mean annual AGWP against mean interval length separately for each plot (Figure 3) and used the resulting gradients to calculate our corrected AGWP estimates for each census interval as follows:

$$AGWP_{corr} = AGWP_{obs} - c*t$$

Where $AGWP_{corr}$ is the corrected mean annual productivity, $AGWP_{obs}$ is the observed mean annual productivity, *c* is the required annual correction (the gradient in Figure 3) and *t* is the census interval length, in years. For four plots in which all consecutive censuses were of greatly different lengths (HCC-23, HCC-24, SUC-03, and TIP-01), we corrected AGWP using the mean *c* derived from all other plots (-0.058).

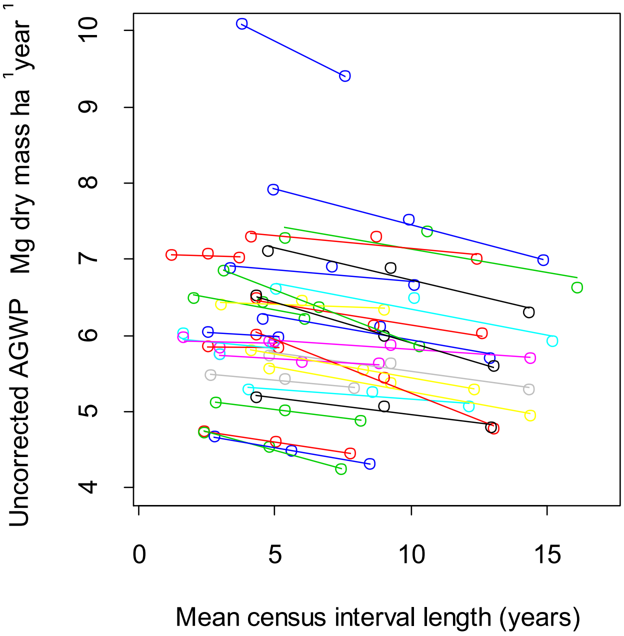

Figure 3: The census interval effect, showing how uncorrected AGWP is higher when census intervals are shorter. Each line represents a single plot, with each point representing the mean uncorrected AGWP of all single censuses, all possible two-census periods, or all possible three-census periods within that plot, excluding consecutive censuses of greatly different lengths (ratios of 1: 3 or greater).

In our second method for census interval correction, denoted '*CIC*$_2$', we used an individual stem-based approach. Since data are collected on the growth of individual stems, the most accurate corrections should be those that use these measurements to estimate the growth both of known stems that die during the interval and of stems that recruit and die unobserved during the interval.

To estimate the growth of known stems that died during the interval, we assumed these stems to have died at the mid-point. We calculated the unobserved growth up to the mid-point using the median growth of all dicotyledonous stems in the plot within the same size class, using the size classes defined above.

We estimated the number of unobserved recruits (U_r) as the product of the number of stems in the plot (N), the time-weighted mean annual mortality rate in the plot (M), the time-weighted mean annual recruitment rate in the plot (R) and the census interval length (t): $U_r = N*M*R*t$. Our use of time-weighted mortality and recruitment estimates representing the entire period across which a plot has been sampled reduces the impact of the variability of these processes over short time-spans. We assumed the diameter growth rate of unobserved recruits to be the median rate for dicotyledonous stems in the 10-19.9 cm size class. We chose this as a lower estimate than the size class mean growth rate or the mean growth rate of recruits, since stems are reported to have reduced growth in the months immediately prior to mortality (Chao et al., 2008). We assigned stem wood density as the same as the plot mean in that census. We assumed these stems recruited on average one-third of the way through the interval and died two-thirds of the way through the interval, allowing growth over a time period equal to one-third of the interval. The estimated unobserved growth from the known stems that died and the unobserved recruits were added to the AGWP of each census interval.

2.3 TREATMENT OF NEWLY RECRUITED STEMS

To estimate AGWP across a census interval, we must include the productivity of trees that surpass our minimum diameter threshold of 10 cm during the census interval, in addition to the gain in AGB of trees that were present at both censuses. The productivity of these new recruits is uncertain, since their diameter is unknown at the start of the census interval. We used three methods to quantify the productivity of new recruits.

For our first method, denoted 'R_1', we assumed the recruits had a diameter of 0 cm in the census prior to recruitment. This is unlikely in practice, but allows the growth of stems <10 cm *D* to be implicitly included in productivity estimates. For this reason it is commonly used. For our second method ('R_2'), we assumed the recruits had a diameter of 10 cm in the census prior to recruitment. Note that to ensure comparability of biomass gain and loss the same 10 cm core must also be subtracted from the biomass of each dead tree when using R_2. These two methods respectively delimit the maximum and minimum possible growth rates of recruited stems. R_1 is used in both our baseline scenario and our suggested scenario.

For our third method ('R_3') we extrapolated the growth rate of each individual stem backwards from the census immediately following recruitment. If the mean of the measured *D* of a newly recruited stem and our extrapolated *D* of the same stem in the previous census was <10 cm, we did not include growth of this stem in our measure of recruitment using R_3 (i.e. we assumed zero growth across the interval for this stem), thereby following equivalent methods to delimit the lower end of the 10-19.9 cm size class as would be used to delimit any other stem size class. Where the plot had no census following recruitment, meaning we could not extrapolate growth rates of recruits, we used the 86th percentile growth rate of stems from the same plot census in the 10-19.9 cm size class, since this was found to provide the closest approximation of the mean growth of recruits. Our mean estimated stem diameter for the census prior to recruitment, excluding stems for which we assumed zero growth as explained above, was 9.74 cm.

3 Results

Our 'baseline scenario' involves ignoring POM changes, ignoring census interval length and assuming the R_1 growth of recruits (from 0 cm diameter), and yields a long-term mean AGWP of 5.44 Mg dry mass ha^{-1} year^{-1} (*n* = 35; Table 1). By contrast, our 'suggested scenario' which incorporates corrections for POM changes (G_3) and census interval length (CIC_2), while retaining R_1 recruitment, gave a mean AGWP estimate of 6.17 Mg dry mass ha^{-1} $year^{-1}$ (13.4% greater). Thus, it appears that disregarding these issues would substantially underestimate the true AGWP of these forest plots.

Table 1: Mean annual AGWP across all plots. Some important combinations of methods are listed first, followed by each possible remaining combination (apart from some involving $G_4/G_5/G_6$*)*

Method	**Treatment of POM change**[a]	**Treatment of recruits**[b]	**Census interval correction**[c]	**Mean annual AGWP across all plots, with bootstrapped 95% confidence intervals (Mg dry mass ha^{-1} $year^{-1}$)**
Baseline scenario	G_1	R_1	*Without CIC*	5.44 (5.12 - 5.79)
Suggested scenario	G_3	R_1	CIC_2	6.17 (5.82 - 6.55)
Using D_{old}	G_4	R_1	CIC_2	6.26 (5.89 - 6.63)
Using D_{new}	G_5	R_1	CIC_2	6.00 (5.66 - 6.34)
After Clark et al., (2013)	G_6	R_1	CIC_2	6.24 (5.87 - 6.61)
A	G_2	R_1	*Without CIC*	5.95 (5.61 - 6.32)
B	G_3	R_1	*Without CIC*	6.01 (5.65 - 6.37)
C	G_1	R_2	*Without CIC*	4.96 (4.65 - 5.29)
D	G_2	R_2	Without *CIC*	5.48 (5.13 - 5.83)
E	G_3	R_2	Without *CIC*	5.53 (5.18 - 5.89)
F	G_1	R_3	*Without CIC*	4.95 (4.64 - 5.29)
G	G_2	R_3	Without *CIC*	5.47 (5.14 - 5.83)
H	G_3	R_3	Without *CIC*	5.52 (5.16 - 5.89)
I	G_1	R_1	CIC_1	5.71 (5.38 - 6.08)
J	G_2	R_1	CIC_1	6.22 (5.87 - 6.60)
K	G_3	R_1	CIC_1	6.27 (5.92 - 6.66)
L	G_1	R_2	CIC_1	5.23 (4.91 - 5.59)
M	G_2	R_2	CIC_1	5.74 (5.40 - 6.10)
N	G_3	R_2	CIC_1	5.79 (5.44 - 6.18)
O	G_1	R_3	CIC_1	5.22 (4.90 - 5.58)
P	G_2	R_3	CIC_1	5.73 (5.39 - 6.10)

Q	G_3	R_3	CIC_1	5.79 (5.43 - 6.17)
R	G_1	R_1	CIC_2	5.61 (5.29 - 5.96)
S	G_2	R_1	CIC_2	6.12 (5.78 - 6.47)
T	G_1	R_2	CIC_2	5.11 (4.81 - 5.45)
U	G_2	R_2	CIC_2	5.63 (5.30 - 5.99)
V	G_3	R_2	CIC_2	5.68 (5.34 - 6.04)
W	G_1	R_3	CIC_2	5.11 (4.79 - 5.45)
X	G_2	R_3	CIC_2	5.62 (5.29 - 5.98)
Y	G_3	R_3	CIC_2	5.68 (5.33 - 6.04)

[a] G_1: No correction for POM changes; G_2: Uses standardised POM height at D_{mean} in all censuses; G_3: Uses combination of diameter at D_{mean} in censuses with POM changes and directly measured diameters in other censuses; G_4: uses diameter at D_{old} in all censuses; G_5: uses diameter at D_{new} in all censuses; G_6: after a POM change the increment at D_{new} is added to the original diameter at D_{old}.

[b] R_1: Assumes recruits have a diameter of 0 cm in the census prior to recruitment; R_2: Assumes recruits have a diameter of 10 cm in the census prior to recruitment; R_3: Extrapolates stem growth rates backwards from the census following recruitment.

[c] CIC_1: Parametric correction for census interval length; CIC_2: Stem-by-stem correction for census interval length.

3.1 EFFECT OF POM CHANGE PROTOCOL

When census-interval corrections and recruitment are treated as in the suggested scenario (CIC_2, R_1), but diameter is used as measured in the field (G_1 protocol), i.e. ignoring the effect of POM changes, estimated mean annual AGWP is 5.61 Mg dry mass ha^{-1} year^{-1}, 9.2% lower than the suggested scenario (which uses G_3). By contrast, if instead growth is based on the mean of growth at the new and old POM (G_2), annual AGWP across our plots is estimated as 6.12 Mg dry mass ha^{-1} year^{-1}, just 0.9% lower than the suggested scenario (Figure 4). Alternatively, using a fixed POM at D_{old} (G_4) produces a mean annual AGWP of 6.26 Mg dry mass ha^{-1} year^{-1}, a fixed POM at D_{new} (G_5) gives 6.00 Mg dry mass ha^{-1} year^{-1}, and adding the diameter increment at D_{new} to the original diameter at D_{old} (G_6) yields 6.24 Mg dry mass ha^{-1} year^{-1}.

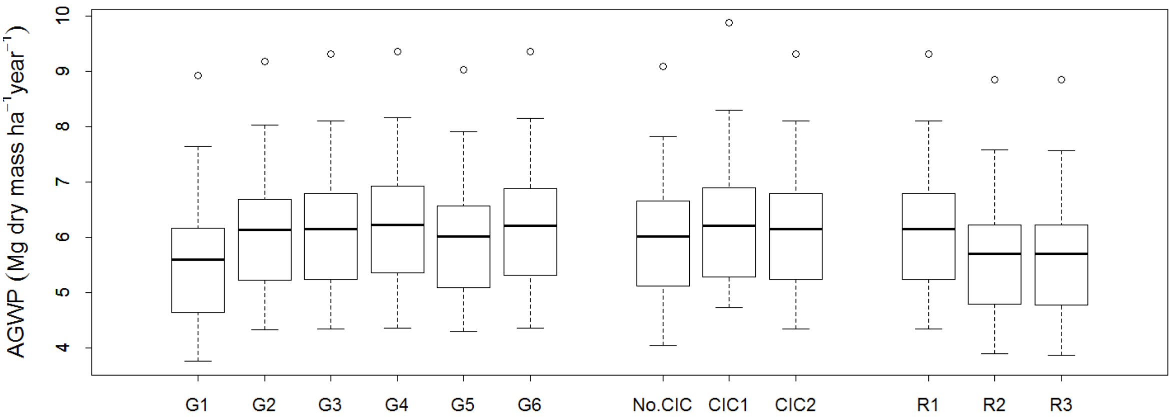

Figure 4: Variation in mean annual AGWP (Mg dry mass ha^{-1} year^{-1}) with method choice. Each group of boxplots shows the effect of changing a single factor, with the other methods based on the standard suggested scenario in which corrections for both POM changes (G_3*) and census interval length (*CIC_2*) have been made. From left to right, the single factors are POM change protocol, method of census interval correction, and treatment of recruits.*

The impact of POM changes is linked to the total length of the sampling period. As trees grow and time elapses, the greater the proportion of stems that will have undergone POM changes. By the final census, on average 16.8 years after the initial census, a mean of 10.5% of stems present have had their POM changed. Nevertheless, the impact of POM changes does not appear to be linked to mean interval length or baseline scenario productivity (SI Figure S1).

3.2 EFFECT OF CENSUS INTERVAL CORRECTION

The length of census intervals also has a noticeable impact on productivity estimates. Without correcting for census interval length, mean AGWP (using G_3 and R_1) is estimated at 6.00 Mg dry mass ha^{-1} year^{-1}, 2.7% less than our suggested stem-by-stem method (CIC_2), which gives an estimate of 6.17 Mg dry mass ha^{-1} year^{-1}. When parametric (CIC_1) rather than stem-by-stem census interval corrections are applied, AGWP is estimated at 6.27 Mg dry mass ha^{-1} year^{-1} (Figure 4).

The corrections applied in each plot using method CIC_1 are shown in Figure 3. Dividing the gradients in this graph by the mean uncorrected AGWP values in each plot, we derive a simple formula that shows the mean proportional annual correction:

$$AGWP_{corr} = AGWP_{obs} + 0.0091\ AGWP_{obs} * t$$

Where $AGWP_{corr}$ is the corrected mean annual productivity and $AGWP_{obs}$ is the observed mean annual productivity within a census interval of length t, in years. This gives a correction of 0.91% per census-interval year. Using either method of census interval correction, the corrections appear closely related to interval length (SI Figure S2).

3.3 EFFECT OF TREATMENT OF RECRUITS

When growth of recruits is assumed to start from 10 cm D at the time of the previous census (R_2), rather than from 0 cm D (R_1), mean AGWP falls 7.9% to 5.68 Mg dry mass ha^{-1} year^{-1} (Figure 4). The difference in estimated AGWP between R_1 and R_2 will be greatest when AGWP is low and when mean interval length is long, since under these circumstances recruits comprise the highest proportion of total wood production (SI Figure S3). Considering solely the productivity of the recruits, with R_1 mean annual AGWP of recruits was 0.73 Mg dry mass ha^{-1} year^{-1}, while switching to R_2 reduced this by 65.7% to 0.25 Mg dry mass ha^{-1} year^{-1}. Back-extrapolation of individual stem growth rates from later censuses (R_3) produces a mean AGWP of 5.68 Mg dry mass ha^{-1} year^{-1}, similar to R_2 and 8.1% lower with R_1, with 0.24 Mg dry mass ha^{-1} year^{-1} for the recruits only.

4 Discussion

We show that the choice of methods for estimating AGWP can have an important impact on the values obtained, with mean AGWP from our baseline scenario and suggested scenario differing by 13.4%. This becomes especially important when estimating AGWP across long periods, since potential sources of bias tend to increase with time. Here we discuss problems related to POM changes, census interval corrections and recruited stems in turn.

Changes in the point of measurement of stems are made in response to buttress growth, but pose a challenge for interpreting long-term tree measurement data. For census intervals with POM changes, use of directly measured diameters as in G_1 does not provide an appropriate measure of growth because it involves comparing diameters at different points along a tapering trunk (Niklas 1995). Using a fixed POM across these intervals (i.e. same measurement height at the start and end of the census), as we did in G_2 and G_3, gives a more appropriate measure of growth. Of all the methodological variants we tested, the greatest single impact on AGWP estimates was caused by incorrect use of G_1 instead of using a protocol to account for the impact of POM changes.

There are several potential methods of correcting for POM changes. In the G_2 protocol, D_{mean} is used for all census intervals, not just those involving POM changes. Our diameter estimates at new POMs for the censuses prior to a POM change, and at old POMs for the censuses following a POM change, rely on the assumption of an unchanging old POM: new POM ratio. This may add some uncertainty, since the degree of stem taper can change during ontogeny (Metcalf et al., 2009), but has the advantage of internal consistency in providing an estimate of tree diameter and growth at an unvarying location through time, and this internal consistency is potentially helpful for analysis of biomass dynamics. Fixing the POM at either D_{old} (G_4) or D_{new} (G_5) is conceptually similar to G_2, with these techniques being, respectively, slightly less or more conservative with regard to growth estimates. Adding instead the diameter increment at D_{new} to the original diameter at D_{old} (G_6, used by Clark et al., (2013)) provides a further means to correct for POM changes that in effect fixes the POM height. The G_3 protocol has the advantage of maximising the use of actual diameter measurements taken in the field (i.e., for all censuses except those involving POM changes) which lends itself to among-site comparisons of stand-level AGWP.

While there are subtle differences between each of these approaches, all five of the POM-change analytical methods produce rather similar estimates of AGWP. All five contrast sharply to the use of directly measured diameters throughout, which clearly underestimates productivity. By contrast to our methods based on stem characteristics, a promising site-specific approach has been developed to deal with these challenges involving species-based Bayesian models to represent stem taper and diameter growth rates (Metcalf et al., 2009), but this is unlikely to be feasible when dealing with large numbers of rare tropical species across multiple sites, for which sufficient data to calibrate stem taper may not be available.

A second set of challenges with deriving AGWP estimates relates to their sensitivity to the length of measurement interval. Most trees that die will nevertheless still have grown since the last census before dying; similarly some trees will both recruit and die, unmeasured, within a single census interval (Sheil & May 1996). The failure to observe the full growth of these stems affects mortality estimates as well as productivity estimates, and when calculating net fluxes corrections can be made to mortality that are equivalent to the corrections to productivity that we present here.

Our two different census-interval correction methods both produced results relatively close to the 0.67% median annual correction (with range 0.04 – 1.39%) derived by Malhi et al., (2004). Of the two methods, the individual-stem based method (CIC_2) has the potential to provide the most accurate corrections, reflecting real fluctuations in mortality rates and making the maximum use of the available data. This method works for a single interval and is not dependent on a large dataset to provide accurate parameter estimates.

Nevertheless, CIC_2 remains subject to uncertainties. Several authors have reported that stems grow at below-average rates in the years or months prior to mortality (Bigler and Bugmann, 2003; Chao et al., 2008; Vasconcelos et al., 2012; Wyckoff and Clark, 2002). Similarly, unobserved recruits that die may have lower than average taxon-level wood density, as this has been shown to be a predictor of mortality (Chao et al., 2008; Kraft et al., 2010). Both these factors may cause our assumed growth in CIC_2 to be too high, although we deal with this by using median growth estimates for the unobserved growth of known stems that die and of unobserved recruits, as explained above. However, there are also reasons suggesting that growth in CIC_2 is underestimated, due to the above-average diameter growth rates typical of high turnover, low wood density species. On balance, since CIC_2 on average gives slightly lower growth than CIC_1, our assumed growth in CIC_2 appears if anything to be slightly conservative.

A third persistent challenge to estimating forest AGWP results from stems in inventory plots not being measured until they reach a certain diameter threshold, one of the most common being 10 cm. Moving to a lower threshold would not benefit the interpretation of existing long-running datasets, and even in inventory plots with 1 cm D thresholds (Chave et al., 2008) the problem remains conceptually equivalent, although the potential range of AGWP values associated with the treatment of recruits is naturally greatly reduced. Assuming growth from 0 cm (R_1) typically overestimates the actual growth of the stem in that interval, since it normally takes many years for a stem to reach a diameter of 10 cm. Backwards extrapolation of growth rates of recruited stems (R_3) produces plot-level AGWP very similar to estimates made assuming growth from 10 cm (R_2). Although R_3 provides the most accurate measure of the growth of an individual recruit across the relevant census interval, it is difficult to ensure comparability of biomass gain and loss using this method, due to the stem-specific minimum diameters used.

In comparison to the other methods, R_1 allows for an implicit partial inclusion of the growth of stems below the minimum diameter threshold. Nevertheless, it must be recognised that AGWP estimates made using R_1 fail to include the productivity of stems that die before reaching 10 cm D (Malhi et al., 2004). For this reason, the R_1 protocol is not equivalent to the use of a lower diameter threshold. Yet R_1 remains a closer approximation of true AGWP (no lower threshold) than our other methods.

Due to the considerations outlined above, the choice of method for correcting the problem of unobserved growth from recruited stems is in some senses more complex than for the other two factors we investigated. On balance, especially if the aim is to provide an approximation of total AGWP and to contribute to estimating stand-level fluxes and stocks, then R_1 is preferred. Method R_2 is suggested in two situations. Firstly, if productivity is being compared to other stand attributes or functions classified by size class, then method R_2 may enable equivalency in the samples used for each variable. Secondly, using R_2 can reduce bias caused by temporal fluctuations in recruitment rates. The accuracy of AGWP estimates made using R_1 depends on the length of time across which mean rates are calculated. If analysing variability in growth rates from one census interval to the next, AGWP may be unduly influenced by the number of stems which happen to pass the 10 cm threshold during a given interval. Therefore R_2 may be preferred for the analysis of short-term variability in AGWP.

5 Conclusion

The protocols described here provide a set of suggested methods for estimating AGWP that can minimise the influence of a number of known time-sensitive biases (relating to POM changes, unobserved growth within census intervals and the treatment of newly recruited stems), and which may be broadly applicable to long-term forest plot data. In western Amazonia these corrections increase estimates of AGWP by 13.4% compared to the baseline scenario in which these measurement problems are ignored. The largest bias observed was that associated with ignoring POM changes which results in large underestimates of AGWP; correction methods differ but tend to provide broadly similar results. Census interval corrections are also often necessary for more accurate AGWP estimation. The associated underestimation of AGWP increases with interval length, thus corrections are needed to compare data from plots with differing census interval lengths. Assumptions relating to recruits depend on the specific question being asked. Assuming recruits grew from 0 cm in the previous census interval likely provides a closer approximation of total AGWP than other methods, but other procedures may be more relevant to the specific questions addressed. Together, we hope these suggested techniques will help to improve the quantification of aboveground coarse woody production and the comparability of future studies.

6 Acknowledgements

Data collection has been supported by grants from the European Union, the UK Natural Environment Research Council, and the Gordon and Betty Moore Foundation. JT is supported by a NERC PhD Studentship with CASE sponsorship from UNEP-WCMC. RJWB is supported by a NERC Research Fellowship; SLL is supported by a Royal Society University Research Fellowship; OLP and SLL are supported by an ERC Advanced Grant "Tropical Forests in the Changing Earth System", and OLP by a Royal Society Wolfson Research Merit Award. We thank Rodolfo Vasquez Martinez and Nallaret Davila Cardozo for contributing their botanical expertise, Georgia Pickavance for her work with the ForestPlots.net database, Lera Miles and Drew Purves for advice, and the many colleagues and field assistants who have contributed to the development of the RAINFOR network.

7 References

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W., Roupsard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I., Papale, D., 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. Science 329, 834–838.

Bigler, C., Bugmann, H., 2003. Growth-dependent tree mortality models based on tree rings. Can. J. For. Res. 33, 210–221.

Blanc, L., Echard, M., Herault, B., Bonal, D., Marcon, E., Chave, J., Baraloto, C., 2009. Dynamics of aboveground carbon stocks in a selectively logged tropical forest. Ecol. Appl. 19, 1397–1404.

Chao, K.J., Phillips, O.L., Gloor, E., Monteagudo, A., Torres?Lezama, A., Martínez, R.V., 2008. Growth and wood density predict tree mortality in Amazon forests. J. Ecol. 96, 281–292.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B., Yamakura, T.,

2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99.

Chave, J., Condit, R., Muller-Landau, H.C., Thomas, S.C., Ashton, P.S., Bunyavejchewin, S., Co, L.L., Dattaraja, H.S., Davies, S.J., Esufali, S., Ewango, C.E.N., Feeley, K.J., Foster, R.B., Gunatilleke, N., Gunatilleke, S., Hall, P., Hart, T.B., Hernandez, C., Hubbell, S.P., Itoh, A., Kiratiprayoon, S., LaFrankie, J.V., de Lao, S.L., Makana, J.R., Noor, M.N.S., Kassim, A.R., Samper, C., Sukumar, R., Suresh, H.S., Tan, S., Thompson, J., Tongco, M.D.C., Valencia, R., Vallejo, M., Villa, G., Yamakura, T., Zimmerman, J.K., Losos, E.C., 2008. Assessing evidence for a pervasive alteration in tropical tree communities. Plos Biol. 6, 455–462.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: Concepts and field methods. Ecol. Appl. 11, 356–370.

Clark, D.A., Clark, D.B., Oberbauer, S.F., 2013. Field-quantified responses of tropical rainforest aboveground productivity to increasing CO2 and climatic stress, 1997–2009. J. Geophys. Res. Biogeosciences.

Condit, R., 1998. Tropical forest census plots. Springer-Verlag, Berlin.

Deans, J.D., Moran, J., Grace, J., 1996. Biomass relationships for tree species in regenerating semi-deciduous tropical moist forest in Cameroon. For. Ecol. Manag. 88, 215–225.

Fang, Z., Bailey, R.L., 1999. Compatible volume and taper models with coefficients for tropical species on Hainan Island in southern China. For. Sci. 45, 85–100.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., et al., 2012. Tree height integrated into pantropical forest biomass estimates. Biogeosciences 9, 3381–3403.

Flores, O., Coomes, D.A., 2011. Estimating the wood density of species for carbon stock assessments. Methods Ecol. Evol. 2, 214–220.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., Zeng, N., 2006. Climate-carbon cycle feedback analysis: Results from the C(4)MIP model intercomparison. J. Clim. 19**,** 3337-3353.

Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L.M., Sitch, S., Fisher, R., Lomas, M., Walker, A.P., Jones, C.D., Booth, B.B.B., Malhi, Y., Hemming, D., Kay, G., Good, P., Lewis, S.L., Phillips, O.L., Atkin, O.K., Lloyd, J., Gloor, E., Zaragoza-Castells, J., Meir, P., Betts, R., Harris, P.P., Nobre, C., Marengo, J., Cox, P.M., 2013. Simulated resilience of tropical rainforests to CO2-induced climate change. Nat. Geosci. 6, 268-273.

King, D., 1981. Tree dimensions: Maximizing the rate of height growth in dense stands. Oecologia 51, 351–356.

Kraft, N.J.B., Metz, M.R., Condit, R.S., Chave, J., 2010. The relationship between wood density and mortality in a global tropical forest data set. New Phytol. 188, 1124–1136.

Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, M.N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., Woll, H., 2009. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006.

Lewis, S.L., Phillips, O.L., Sheil, D., Vinceti, B., Baker, T.R., Brown, S., Graham, A.W., Higuchi, N., Hilbert, D.W., Laurance, W.F., Lejoly, J., Malhi, Y., Monteagudo, A., Núñez Vargas, P., Sonké, B., Supardi, N., and TERBORGH, J.W., Vásquez Martínez, R., 2004. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. J. Ecol. 92, 929–944.

Lewis, S.L., Sonké, B., Sunderland, T., Begne, S.K., Lopez-Gonzalez, G., et al., 2013. Above-ground biomass and structure of 260 African tropical forests. Philos. Trans. R. Soc. B Biol. Sci. 368.

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M., Phillips, O.L., 2011. ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. J. Veg. Sci. 22, 610–613.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B., Lloyd, J., 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Glob. Change Biol. 10, 563–591.

Malhi, Y., Doughty, C., Galbraith, D., 2011. The allocation of ecosystem net primary productivity in tropical forests. Philos. Trans. R. Soc. B Biol. Sci. 366, 3225–3245.

Martin, A.R., Thomas, S.C., 2011. A reassessment of carbon content in tropical trees. PLoS ONE 6, e23533.

Metcalf, C.J.E., Clark, J.S., Clark, D.A., 2009. Tree growth inference and prediction when the point of measurement changes: modelling around buttresses in tropical forests. J. Trop. Ecol. 25, 1–12.

Niklas, K.J., 1995. Size-dependent allometry of tree height, diameter and trunk-taper. Ann. Bot. 75, 217–227.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993.

Phillips, O., Baker, T., Feldpausch, T.R., Brienen, R.J.W., 2009a. RAINFOR field manual for plot establishment and remeasurement.

http://www.rainfor.org/upload/ManualsEnglish/RAINFOR_field_manual_version_June_2009_ENG.pdf. Accessed 31/10/2013.

Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., et al., 2009b. Drought sensitivity of the Amazon rainforest. Science 323, 1344–1347.

Poorter, L., Werger, M.J.A., 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. Am. J. Bot. 86, 1464–1473.

Sheil, D., 1995. A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. For. Ecol. Manag. 77, 11–34.

Sheil, D., May, R.M., 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. J. Ecol. 84, 91–100.

TEAM Network, 2010. Vegetation protocol implementation manual, v1.5. Tropical Ecology, Assessment and Monitoring Network, Science and Knowledge Division, Conservation International, Arlington, VA, USA.

Tian, H., Melillo, J.M., Kicklighter, D.W., McGuire, A.D., Helfrich, J.V.K., Moore, B., Vörösmarty, C.J., 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. Nature 396, 664–667.

Vasconcelos, S.S., Zarin, D.J., Araújo, M.M., Miranda, I. de S., 2012. Aboveground net primary productivity in tropical forest regrowth increases following wetter dry-seasons. For. Ecol. Manag. 276, 82–87.

Wyckoff, P.H., Clark, J.S., 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. J. Ecol. 90, 604–615.

Zanne, A.E., Lopez Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Global wood density database. *Dryad. Identifier: http://hdl.handle.net/10255/dryad*.